

Effect of seed mass on early seedling growth of five eastern white pine (*Pinus strobus* L.) families under contrasting light environments

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Abstract: The strong influence of seed mass on early seedling growth of forest tree species is well established, but the ecological role of intraspecific variation in seed mass on natural regeneration is poorly understood. Wide variation in initial spatial patterns of natural regeneration of eastern white pine (*Pinus strobus* L.) between managed and undisturbed white pine forests of the Great Lakes region of North America has been attributed to differences in understory light levels and the frequency of substrates suitable for germination and seedling establishment. To explore the potential influence of seed mass on these observed patterns, the interaction of seed mass and light on early growth of white pine was investigated in a greenhouse study. Seedlings of five half-sib families differing in mean seed mass were grown for 8 and 14 weeks under moderate and low light conditions representing managed and undisturbed pine stands, respectively. Family differences in seedling biomass and root system development under each light environment were associated with positive, linear relationships with mean seed mass. Family and seed mass had a comparatively weak influence on biomass partitioning and relative growth rate. Moderate light improved seedling growth regardless of seed mass, but relative expression of seed mass effects on seedling traits was unaffected by light environment. These results suggest differential recruitment of white pine in managed and undisturbed stands is unrelated to variation in seed mass.

Key words: biomass allocation, eastern white pine, greenhouse experiment, natural regeneration, relative growth rate, seed mass.

Résumé : La forte influence de la masse des graines sur le début de la croissance des plantules d'arbres forestiers est bien connue, mais le rôle écologique de la variation intraspécifique de la masse des graines sur la régénération naturelle demeurent mal comprise. Chez le pin blanc (*Pinus strobus* L.), on observe une grande variation des patrons initiaux de régénération naturelle, entre les forêts aménagées et les forêts nonperturbées, de la région des Grands lacs, en Amérique du Nord. On a attribué ces variations au degré de luminosité sous la canopée et à la présence de substrats propices à la germination et à l'établissement des plantules. Afin d'explorer l'influence potentielle de la masse des graines sur ces patrons observés, les auteurs ont étudié l'interaction de la masse des graines et de la lumière sur la croissance initiale du pin blanc, en serres. Ils ont cultivé les plantules de cinq familles de demi-frères, différentes en terme de masse moyenne des graines, pendant 8 et 14 semaines, sous des conditions de luminosité modérée et faible, représentant des peuplements de pins aménagés ainsi que nonperturbés, respectivement. Les différences selon les familles, quant à la biomasse des plantules et au développement du système racinaire, sous chacun des traitements lumineux, montrent des relations linéaires positives avec la masse moyenne des graines. La famille et la masse des graines ont un effet comparativement faible sur la partition des biomasses et sur le taux relatif de croissance. Une luminosité modérée améliore la croissance des plantules, indépendamment de la masse des graines, mais l'expression relative des effets de la masse des graines sur les caractères des plantules n'est pas affectée par l'environnement lumineux. Ces résultats suggèrent que le recrutement différentiel du pin blanc dans les peuplements aménagés versus nonperturbés ne serait pas relié à la masse des graines.

Mots clés : allocation de la biomasse, pin blanc de l'est, expérience en serres, régénération naturelle, taux relatif de croissance, masse des graines.

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Introduction

Seed size is an important plant trait that strongly influences the dispersal, establishment, and survival of plant offspring (Harper et al. 1970). Differences in seed mass among species may span several orders of magnitude within a plant community, with species that have a higher maternal investment in seed tissues generally producing fewer seeds (Harper et al. 1970; Primack 1987; Shipley and Dion 1992; Leishman 2001). The general inverse relationship between the number and mass of seeds produced can be viewed as a tradeoff between competition and colonization (Westoby et al. 1996; Leishman 2001). When grown in competition with smaller-seeded species, species with larger seeds have the advantage of higher metabolic support to early growth and greater seedling size, which improves their establishment (Gross 1984; Wulff 1986; Leishman 2001). Larger-seeded species also exhibit superior establishment in resource-limited, competitive habitats, enhanced emergence from deep litter layers, and greater tolerance of dense shade and defoliation (Salisbury 1942; Leishman and Westoby 1994; Westoby et al. 1996; Leishman 2001).

In contrast, smaller-seeded species exhibit better establishment in open, disturbed habitats, where they require fewer seed resources for early growth (Salisbury 1942; Grime 2001). The higher mean relative growth rates (RGR) of these species may compensate somewhat for the lower support to early growth provided by smaller seed reserves (Shipley and Peters 1990; Cornelissen et al. 1996; Reich et al. 1998; Wright and Westoby 1999). In undisturbed, shaded habitats, seedlings of small-seeded species are overtopped by their larger-seeded counterparts, reducing establishment success. This competitive disadvantage may be balanced by their adaptation for colonization. The production and dispersal of large amounts of seed over a higher fraction of available sites may increase the likelihood of some seeds landing and becoming established on suitable microsites where large seeds are absent (Grime 2001).

Intraspecific variation in seed mass, albeit comparatively narrow, also commonly occurs in herbaceous and woody species (Harper et al. 1970; Michaels et al. 1988) because of positional, environmental, physiological, and genetic factors influencing seed development (McGinley et al. 1987; Michaels et al. 1988). Variation in seed mass within and among individuals of the same species strongly affects seedling size and survival, which may be modified by the growth environment (Weis 1982; Stanton 1984; Wulff 1986; Tripathi and Khan 1990; Khurana and Singh 2000, 2004; Paz and Martínez-Ramos 2003). Ecological correlates for intraspecific variation in seed mass have also been reported, with seedlings from larger seeds having better emergence, growth, and survival under the environmental hazards of closed vegetation, while seedlings from smaller seeds have higher RGR and improved establishment in more open vegetation (Zimmerman and Weis 1983; Gross 1984; Winn 1985; Wulff 1986; Bonfil 1998; Paz and Martínez-Ramos 2003). Since the optimal seed size for establishment differs with microsite conditions, dispersal of seed with a broad range in mass may increase the probability of successful establishment in heterogeneous environments (Janzen 1977; Michaels et al. 1988).

In boreal and temperate coniferous forest tree species, increased seed mass generally affects germination performance slightly and has a short-lived, positive influence on seedling size (Bonner 1987; Farmer 1997). However, most information on seed mass effects within these species is derived from early research that focused on reforestation and on the height and diameter of seedlings produced under near-optimal growth conditions (Righter 1945; Bonner 1987). Comparatively little research has addressed how seed mass influences seedling morphology, RGR, and biomass partitioning and how these relationships may vary with microsite (Wrzeońewski 1982; Wright et al. 1992; Surles et al. 1993; Reich et al. 1994; Wang et al. 1995).

Eastern white pine (*Pinus strobus* L.) is an ecologically and commercially important species of the Great Lakes region of North America; however, its abundance across the landscape has decreased dramatically since European settlement (Wendel and Smith 1990; Frelich 2002). Natural disturbance by recurrent, low- to moderate-intensity wildfire likely favoured regeneration and maintained white pine dominated ecosystems by consuming forest floor organic layers, reducing competing vegetation, and improving the understory light environment, while retaining a seed source in the overstory (Heinselman 1981; Frelich 2002). Poor seedling recruitment in unmanaged, closed-canopy white pine stands in which disturbance by fire has been eliminated has been attributed to heavy shade and a lack of suitable seedbeds, rather than insufficient seed (Carleton et al. 1996; Frelich 2002; Dovčiak et al. 2003). Current white pine management typically involves partial overstory harvesting (i.e., shelterwoods) and a forest floor treatment to emulate fire and create the mineral soil seedbed and understory light levels (ca. 50% of full sunlight) needed for successful natural regeneration of this intermediately shade-tolerant species (Wendel and Smith 1990; Pinto 1992).

White pine dominated stands may produce up to 2.5 million viable seeds·ha⁻¹, with seed mass varying two- to three-fold among and within individuals (Wright 1945; Wendel and Smith 1990). The relationship of white pine seed mass with seed germination and seedling growth has been examined previously (Mitchell 1939; Spurr 1944; Pauley et al. 1955; Genys 1968; Demeritt and Hocker 1975). However, some of the results of this earlier work are inconsistent and difficult to interpret because of differences in methods, growth environment, lack of seed stratification, the number and composition of seedlots tested, and embryo maturity. For example, Spurr (1944) reported a higher percentage of germination for large as opposed to small seeds, while Wright (1945) observed higher germination in medium-mass seedlots than in large- and small-mass seedlots. As well, the influence of light or other resources on seed mass relationships for white pine has not been investigated.

A greenhouse study was initiated to examine the influence of seed mass on early seedling growth, morphology, and biomass partitioning under two light levels that represent the understory of shelterwoods and undisturbed, closed-canopy white pine stands. Sound, fully formed seed from five half-sib families was used to eliminate some of the possible sources of variation in past studies on this species. We assumed that any competitive advantage of larger seed mass would be more fully expressed under the moderate light

level in which white pine natural regeneration is most successful. This assumption provided the basis for formally testing the following hypotheses: (i) moderate light enhances seed mass effects on seedling size, (ii) in larger seeds, more biomass is allocated to photosynthetic tissues, and (iii) higher RGR in seedlings from smaller seeds does not fully compensate for the size advantage of larger-seeded individuals.

Materials and methods

Seed source and processing

White pine seed was collected from 195 trees in two adjacent second-growth, mixed pine-hardwood stands near Grundy Lake Provincial Park (45°56'N, 80°30'W) in central Ontario in September of 1996, a year of above-average seed production. More than 200 seeds from each tree were X-rayed to identify sound seed (Simak 1980). Average seed mass per parent tree was determined by bulk measurement of a known amount (≥ 100) of sound seed. Five half-sib families with bulk-averaged seed mass ranging from 13.6 to 26.6 mg were selected for study. The mass of individual seeds ($n = 100$) was determined for each selected family. One-way analysis of variance (ANOVA) and a Fisher's least significant difference test indicated seed mass differed significantly ($p < 0.05$) among all families (Parker et al. 2005). Stratified seeds ($n = 400$) for each family were germinated under optimal environmental conditions in the laboratory in February 1998 as described in Parker et al. (2005). Germination, defined as radicle protrusion and geotropic curvature, was assessed every 2–3 d for 28 d.

Greenhouse environment

Seedlings were grown from early February to mid-May 1998 in two adjacent, environmentally controlled greenhouse cubicles. Greenhouse lighting was provided by natural sunlight and high-pressure, sodium-vapour lamps. Each cubicle contained two benches, each divided into moderate and low light environments. The low light environment was created using a wood frame structure covered with spectrally neutral shade cloth that reduced transmittance of ambient photon flux density (PFD) by 50%. Mean daily PFD as a percentage of full sunlight for each light environment was estimated using a LI-191SA Line Quantum sensor (LI-COR Inc., Lincoln, Nebraska) and the method of Messier and Puttonen (1995). The mean daily PFD of the shaded locations averaged 12.6%, creating a low light treatment. The unshaded locations had an average PFD of 47.2%, hereafter referred to as the moderate light treatment. The PFD values for the moderate and low light treatments were similar to those reported beneath uniform shelterwoods and closed canopy stands, respectively, in white pine dominated forests in central Ontario (Burgess and Wetzel 2000; W.C. Parker, unpublished data). Mean daily PFD in the moderate light treatment was adequate to support vigorous shoot growth of white pine seedlings, while light intensity beneath shade structures is associated with reduced seedling growth and mortality (Logan 1966; Kobe et al. 1995; Canham et al. 1996; Groninger et al. 1996).

Two 45-celled planting containers per family were randomly placed in each light environment on four benches,

yielding 16 containers per family. Planting cells (volume 98 cm³, depth 122 mm) were filled with 2:1 peat-vermiculite (v/v) potting medium. Blackout curtains and supplemental lighting were used to provide a 14-h photoperiod. Air temperature in the light-dark period was maintained at 25:15 °C. Containers were randomly repositioned every 10 d to minimize the effects of any microenvironmental gradients existing in the greenhouse.

Seed sowing and seedling measurements

Laboratory germination for single families was uniformly high ($\geq 96\%$), with 85%–95% of total germination occurring within a 4-d period. Upon germination, seeds were planted to a depth of ~0.5 cm, with care taken not to damage emerging radicles. Planting cells were then covered with ~2 mm of stone grit to reduce surface drying. Laboratory germination for all families was relatively rapid, and more than 90% of the germinants sown were within a 4- to 5-d period. To further minimize variation in seedling age among containers, germinants of a given family were planted sequentially, one per container. Only 15 uniformly spaced cells were sown in each container to provide adequate space for shoot growth. The number of days until emergence (i.e., appearance of hypocotyl breaking soil surface) was noted for each germinant. Since germination occurred under laboratory conditions and germinants differed in radicle length at time of sowing, seed mass effects on emergence were not formally tested. However, emergence occurred within 4–5 d of sowing for all families and was similar between light environments. Seedlings were watered as needed to keep soil moisture near field capacity.

After 8 and 14 weeks of growth, seedlings ($n = 15$) growing in one container per family were harvested from each bench and light environment. For both growth periods, shoots of neighbouring seedlings within a container did not overlap, and no seedlings were found to be pot bound. Root systems were gently washed free of soil to measure primary root length (maximum vertical extension of the root system) and the number of first-order lateral roots ≥ 1 cm in length (FOLR). Roots, stems, and foliage were dried separately at 70 °C to a constant dry mass to determine biomass components. A significant linear relationship was exhibited between seedling dry mass and leaf, root, and stem dry mass for each light and family combination. The relative partitioning of seedling biomass was calculated as the ratio of organ to total seedling biomass ($\text{g} \cdot \text{g}^{-1}$) and reported as leaf mass ratio (LMR), stem mass ratio (SMR), and root mass ratio (RMR).

Mean RGR was calculated for the two growing periods. Mean RGR was calculated as $(\ln W_2 - \ln W_1) / (t_2 - t_1)$ where W_2 and W_1 are mean seedling biomass ($n = 12$ –15) of a single planting container at the end and start of the growth period ($t_2 - t_1$), respectively. For the initial 8-week growth period, mean seed mass per family was used for W_1 values. The sowing sequence, slightly different sowing dates among germinants, and relatively long growth periods likely minimized any age-related effects on RGR.

Statistical analysis

Preliminary analysis of descriptive statistics and a Shapiro-Wilk test indicated that all variables were normally

Table 1. Significance probability (*p*) values for light (L), family (F), and light × family (L × F) treatment effects on biomass components, root development, biomass partitioning coefficients, and relative growth rate for 8- and 14-week-old white pine seedlings.

Treatment	Leaf dry mass	Stem dry mass	Root dry mass	Total dry mass	RL	FOLR	LMR	SMR	RMR	RGR
8 weeks										
L	0.001	0.006	0.002	0.001	0.041	0.001	0.201	<0.001	<0.001	<0.001
F	<0.001	<0.001	<0.001	<0.001	0.001	<0.001	0.158	<0.001	0.085	0.487
L × F	0.026	0.005	0.001	0.006	0.827	0.007	0.034	0.013	0.406	0.653
14 weeks										
L	0.006	0.004	<0.001	0.002	<0.001	<0.001	0.051	<0.001	0.002	0.001
F	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.004	<0.001	0.251
L × F	0.032	0.004	<0.001	0.005	0.008	0.278	0.013	0.172	0.047	0.687

Note: RL, root length; FOLR, number of first-order lateral roots; LMR, leaf mass ratio; SMR, stem mass ratio; RMR, root mass ratio; RGR, seedling relative growth rate.

distributed, with the exception of FOLR of 8-week-old seedlings. The effects of family and light environment on seedling biomass components, root length, FOLR at 14 weeks, biomass partitioning coefficients, and RGR were analyzed using the GLM procedure of SAS (SAS Institute Inc., v 6.0, Cary, North Carolina), ANOVA, and a split-plot experimental design, with light treatment representing the whole plot and family being the subplot (Anderson and McLean 1974). A mixed general linear model

$$[1] \quad Y_{ijkl} = \mu + B_i + L_j + BL_{ij} + F_k + BF_{jk} + LF_{jk} + BLF_{ijk} + e_{(ijkl)}$$

with light environment (L) and family (F) classified as fixed factors and block (B) (i.e., bench) as a random factor ($p < 0.05$). Analysis of a preliminary model that included greenhouse cubicle as a random factor indicated cubicle effects were negligible. This term was dropped from the model to increase the power of *F* tests for light, family and light × family treatment effects. Analysis of residuals indicated error terms were normally distributed and exhibited constant variance. This model accounted for about 46% of the variation in LMR and ≥76% of variation in remaining variables. The block term was dropped from the model to test for treatment effects on RGR and accounted for ≥82% of variation in this variable. Treatment effects on FOLR of 8-week-old seedlings were analyzed using a nonparametric approach, wherein ANOVA was performed on FOLR observations that were first ranked within blocks (Glantz 1992).

The CORR procedure of SAS (SAS Institute Inc., v 6.0) and Pearson product moment correlation coefficients were used to quantify the relationships of seed mass with seedling morphology, biomass partitioning coefficients, and RGR. Linear regression analysis and the REG procedure of SAS (SAS Institute Inc., v 6.0) were used to quantify the absolute and relative (i.e., dependent variables expressed as a proportion of that for the family with the largest seed mass) effect of light on the relationship of seed mass with seedling traits. Differences in the slope of separately fitted linear regression equations for the two light treatments were tested using the method of Neter and Wasserman (1974). Differences in absolute slope value reflect the influence of light treatment on seedling growth, regardless of seed mass. By comparison, differences in the slope of the proportional change in seed-

ling traits with seed mass are a measure of the relative strength with which seed mass effects are expressed in different light environments.

Results

Light environment did not influence survival, which averaged $97.2 \pm 0.8\%$ and $96.8 \pm 1.5\%$ under moderate and low light, respectively, over the 14-week growth period. Light environment had a significant effect on seedling dry mass components, root length, FOLR, and biomass partitioning after 8 and 14 weeks of growth (Table 1). Low light reduced seedling biomass and root development and increased biomass allocation to shoot production (Figs. 1–3). Biomass allocation patterns also differed with seedling age, with leaf and stem growth being favoured over root growth during the first 8 weeks (Fig. 3). Root growth was higher during weeks 9–14, with LMR and SMR decreasing and RMR increasing in both light environments. As a result, leaf and stem biomass roughly doubled between 8 and 14 weeks of growth, while root biomass increased 10-fold during this period (Fig. 1).

Family had a significant effect on leaf, stem, root, and total seedling dry mass, and root length of 8- and 14-week-old seedlings that was linearly related to seed mass in both light environments (Table 1; Figs. 1, 2). Leaf and seedling dry mass more than doubled, root dry mass was nearly four times higher, and stem dry mass was 30%–60% higher over the full range in seed mass in both light environments. Root morphology was largely independent of seed mass, with a significant linear relationship existing between the number of FOLR and seed mass for only 8-week-old seedlings grown under moderate light (Fig. 2).

Family effects on biomass allocation and its relationship with seed mass were comparatively smaller than those observed for other seedling traits. Family had a significant effect on SMR but not LMR or RMR in 8-week-old seedlings (Table 1; Fig. 3), but biomass partitioning coefficients were largely unrelated to seed mass or seedling dry mass (Table 2). Although seed mass and LMR under moderate light were negatively correlated, investment into foliage decreased by only about 3% over the full range of mean seed mass (Table 2; Fig. 3). Family differences in biomass partitioning

Fig. 1. Relationship of seed mass with mean ($\pm$ SE) leaf dry mass (a, b), stem dry mass (c, d), root dry mass (e, f), and total seedling dry mass (g, h) for seedlings from five families grown for 8 (a, c, e, g) and 14 (b, d, f, h) weeks under moderate ($\circ$) and low ($\bullet$) light. Linear regression equations and coefficients of determination (r^2) are presented for relationships under moderate (M) and low (L) light. Bolded r^2 values indicate a significant linear relationship ($p < 0.05$) between seed mass and a seedling variable within a given light treatment. Asterisks following a regression equation signify a significant difference ($p < 0.05$) in slope between light treatments for a given seedling variable. A regression equation followed by "ns" indicates the absence of a significant difference in slope.

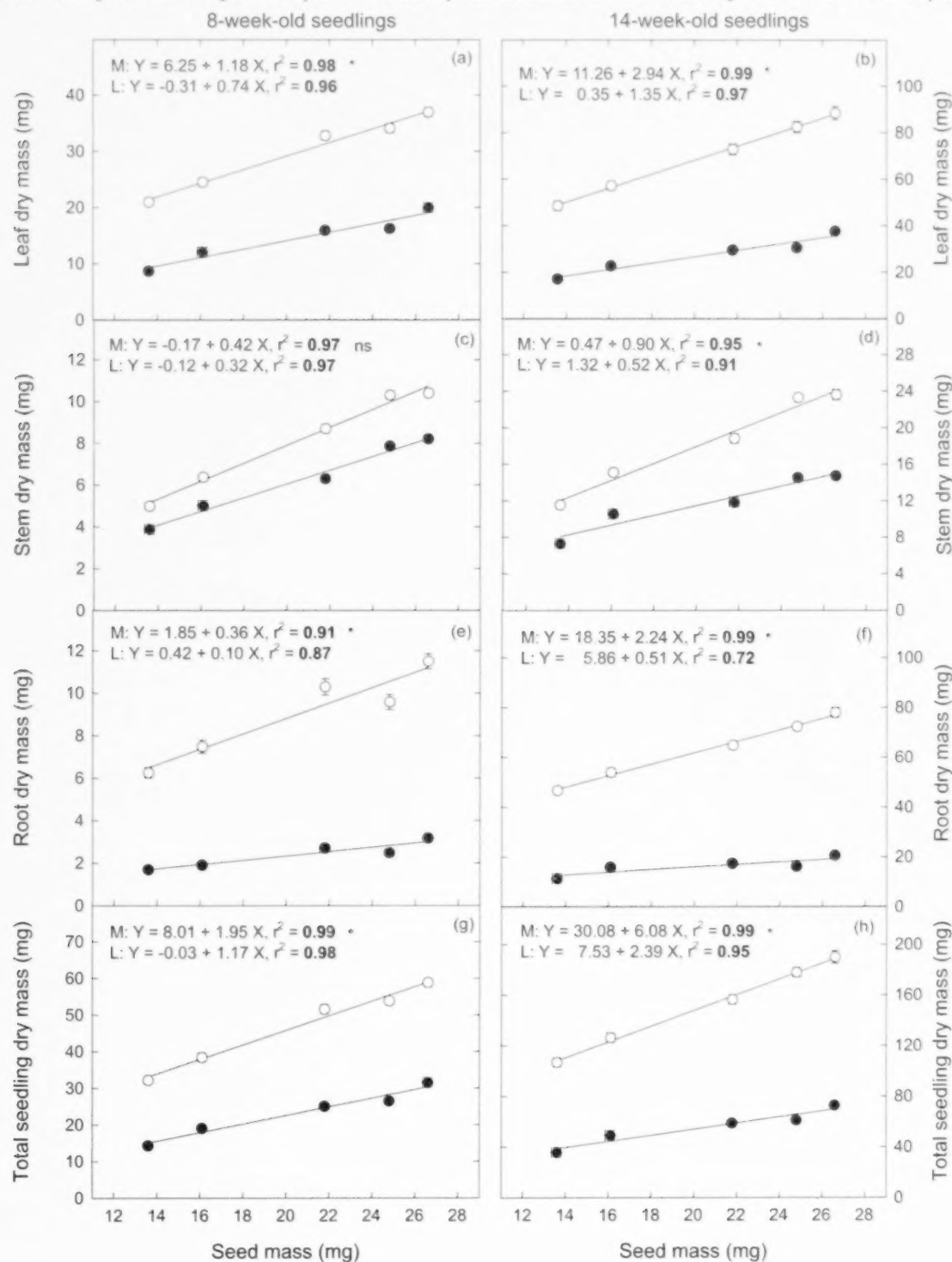
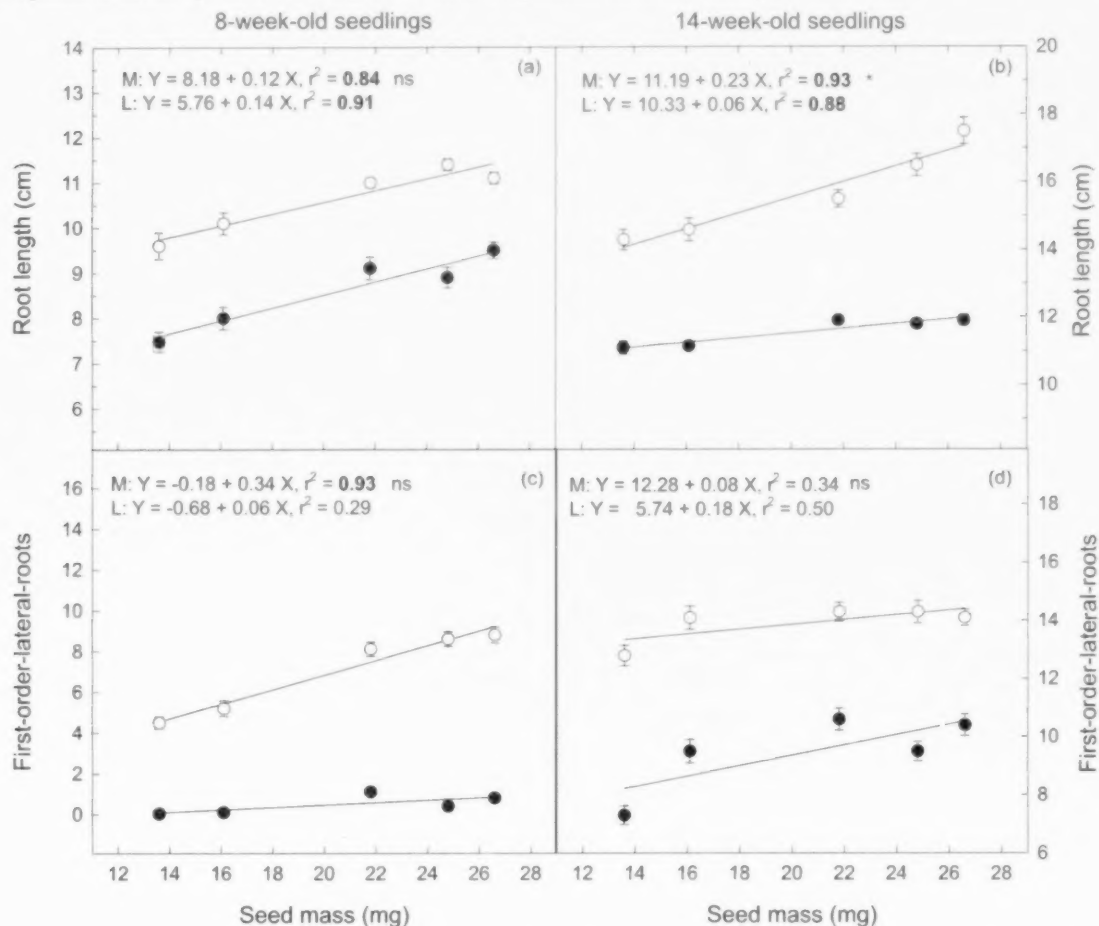


Fig. 2. Relationship of seed mass with mean ($\pm$ SE) primary root length (*a, b*) and number of first-order lateral roots (*c, d*) for seedlings from five families grown for 8 (*a, c*) and 14 (*b, d*) weeks at moderate ($\circ$) and low ($\bullet$) light. Linear regression equations and coefficients of determination (r^2) are presented for relationships under moderate (M) and low (L) light. Bolded r^2 values indicate a significant linear relationship ($p < 0.05$) between seed mass and a seedling variable within a given light treatment. Asterisks following a regression equation denote a significant difference ($p < 0.05$) in slope between light treatments for a given seedling variable. A regression equation followed by "ns" indicates the absence of a significant difference in slope.



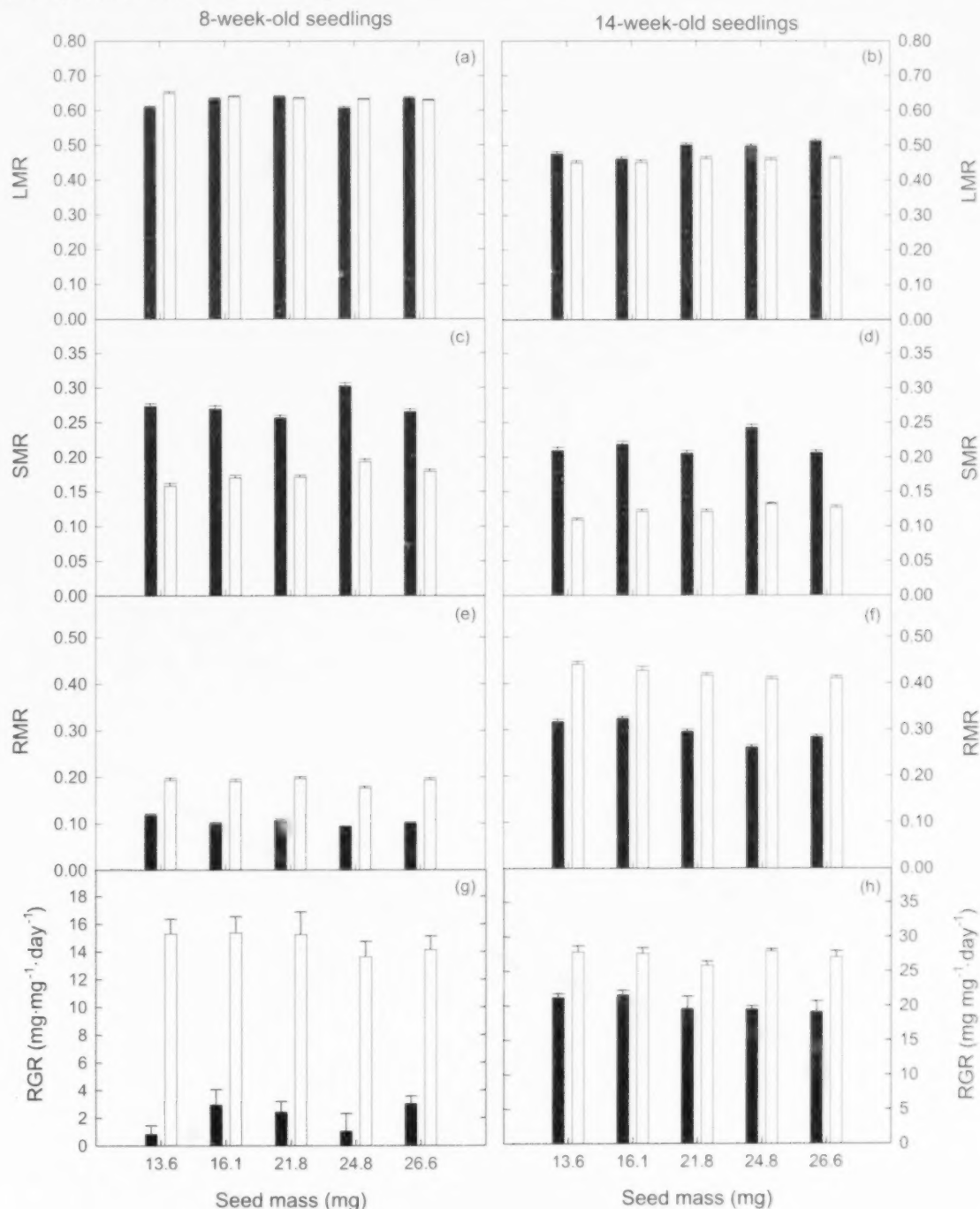
were more strongly related to seed mass in 14-week-old seedlings, with LMR increasing and RMR decreasing with seed mass in both light environments (Tables 1, 3). In seedlings of families with the heaviest and lightest seeds, leaf mass ratio differed by 8% and 3%, and RMR differed by 18% and 8%, under low and moderate light, respectively. In both light environments, higher LMR and lower RMR were associated with greater dry mass of 14-week-old seedlings.

Significant light $\times$ family treatment effects were exhibited for most seedling biomass components, with low light diminishing seed mass effects on seedling size (Table 1; Fig. 1). Significantly larger slope values for the linear relationship of seedling and component biomass with seed mass indicated that the absolute gain in leaf, stem, root, and seedling dry mass per unit increase in mean seed mass was comparatively larger in moderate light, although this trend varied slightly between 8- and 14-week-old seedlings (Fig. 1). Light treatment had much less effect on the relationship between root development and seed mass, but the change in root length per unit seed mass of 14-week-old seedlings was

larger under moderate light (Fig. 2). Light did not affect the comparatively weak relationships of biomass partitioning coefficients with seed mass (Fig. 3). However, the proportional change in seedling features with seed mass did not differ between light treatments (data not shown) indicating that the expression of seed mass effects was unaffected by light.

The RGRs of 8- and 14-week-old seedlings were significantly higher under moderate light, did not differ among families, and had little relationship with seedling dry mass, biomass allocation patterns, and seed mass (Tables 1–3; Fig. 3). Relative growth rate influenced seedling dry mass only for 8-week-old seedlings grown under low light. This higher RGR was associated with increased allocation to foliage and lower investment in stem production (Table 2). Under moderate light, higher RGR of 8-week-old seedlings was associated with lower SMR and higher RMR but not with seedling dry mass. Relative growth rate was significantly correlated with seed mass only for 14-week-old seedlings grown under low light, when the family with the smallest

Fig. 3. Relationship of seed mass with mean ($\pm$ SE) leaf mass ratio (LMR; *a, b*), stem mass ratio (SMR; *c, d*), root mass ratio (RMR; *e, f*), and seedling relative growth rate (RGR; *g, h*) for seedlings from five families grown for 8 (*a, c, e, g*) and 14 weeks (*b, d, f, h*) in moderate (open bars) and low (solid bars) light.



seed mass had a 9% higher RGR than the family with largest seed mass (Table 3).

Discussion

The results of our greenhouse study suggest that under

nonlimiting soil resources, white pine seedlings from larger seeds have greater initial size after 8 and 14 weeks of growth. This size advantage may enable seedlings to compete more effectively in an emerging or existing understory canopy, thereby improving establishment under shade (Wilson 1988). The strong influence of seed mass on early

Table 2. Pearson product moment correlation coefficients for selected traits of 8-week-old white pine seedlings; upper and lower half of matrices refer to seedlings grown under low and moderate light, respectively.

	Seed mass	RGR	LMR	SMR	RMR	Total dry mass
Low light						
Seed mass		0.28	0.25	0.16	-0.69	0.98*
RGR	-0.81		0.73*	-0.85*	0.37	0.50*
LMR	-0.96*	0.38		-0.84*	-0.10	0.40
SMR	0.79	-0.75*	-0.61		-0.44*	-0.26
RMR	-0.28	0.47*	-0.36	-0.52*		-0.19
Total dry mass	0.99*	0.26	-0.27	0.14	0.13	
Moderate light						

Note: Each observation for correlations with mean seed mass is the mean value of four multipot containers per family. All other correlations are based on seedling mean values for 20 individual multipot containers (four containers per family and 12–15 seedlings/container). LMR, leaf mass ratio; SMR, stem mass ratio; RMR, root mass ratio; RGR, seedling relative growth rate.

*Significant at $p < 0.05$.

Table 3. Pearson product moment correlation coefficients for selected traits of 14-week-old white pine seedlings; upper and lower half of matrices refer to seedlings grown under low and moderate light, respectively.

	Seed mass	RGR	LMR	SMR	RMR	Total dry mass
Low light						
Seed mass		-0.94*	0.90	0.20	-0.89*	0.97*
RGR	-0.29		-0.06	-0.40	0.39	0.04
LMR	0.91*	0.30		-0.46*	-0.70*	0.71*
SMR	0.85	-0.16	-0.39		-0.30	-0.34
RMR	-0.97*	-0.26	-0.94*	0.04		-0.48*
Total dry mass	0.99*	0.19	0.59*	0.25	-0.73*	
Moderate light						

Note: Each observation for correlations with seed mass is the mean value of four multipot containers per family ($n = 5$). All other correlations are based on mean values for 20 individual multipot containers (four containers per family and 12–15 seedlings/container). LMR, leaf mass ratio; SMR, stem mass ratio; RMR, root mass ratio; RGR, seedling relative growth rate.

*Significant at $p < 0.05$.

growth was the result of larger embryo and reserve tissues in heavier seeds, since virtually all seedlings emerged within a 4- to 5-d period. Earlier studies of white pine have attributed positive seed mass effects on seedling size and biomass components to larger reserve tissues and (or) earlier emergence of larger seeds (Mitchell 1939; Spurr 1944; Pauley et al. 1955; Demeritt and Hocker 1975). The larger absolute increase in seedling biomass per unit seed mass under moderate light conditions was due primarily to the comparatively higher RGR at higher PFD. However, the proportional change in seedling mass with seed mass was independent of light conditions, indicating that light availability did not alter expression of seed mass effects. Therefore, our results do not support our hypothesis that larger seed mass in white pine is more adaptive under the moderate light conditions of partial overstory canopies.

Despite ontogenetic shifts in biomass partitioning, shoot production in 8- and 14-week-old seedlings was favoured over root production under low light. Preferential investment in shoot production in white pine grown under low light has

been observed previously (Canham et al. 1996; Groninger et al. 1996; Reich et al. 1998), presumably resulting in a shoot–root balance adaptive to shaded microhabitats. Seed mass had a comparatively minor effect on biomass partitioning, which was more strongly expressed in older seedlings. The higher LMR and lower RMR observed after 14 weeks in families with heavier seed under both moderate and low light were associated with a higher shoot/root ratio and greater seedling dry mass. These findings provide weak evidence for our second hypothesis that seed mass is positively related to production of photosynthetic tissues. Higher investment in leaf as opposed to root tissue production may increase the shade tolerance of seedlings from larger seeds by increasing light harvest, photosynthetic capacity, carbohydrate reserves, and the potential to replace tissues lost to pathogens and herbivores. Larger seed mass was also associated with a higher shoot/root ratio in seedlings of *Pinus banksiana* L., *Albizia procera* Benth., *Banksia cunninghamii* Sieber ex Rchb., and *B. marginata* Cav. (Wright et al. 1992; Khurana and Singh 2000; Vaughton and Ramsey 1998,

2001) but was unrelated to allocation patterns in *Pinus sylvestris* L. (Reich et al. 1994) and *Picea mariana* (Mill.) BSP (Wang et al. 1995).

Seedling RGR varies among plant species and is dependent on environmental factors, numerous plant characters, and age (Lambers and Poorter 1992; Walters et al. 1993; Reich et al. 1998; Walters and Reich 2000). Over both growth periods, RGR of white pine seedlings was substantially reduced by low light, similar to the results of Walters et al. (1993). Relative growth rate of 8-week-old seedlings was correlated with biomass partitioning coefficients but was independent of allocation patterns in the 14-week-old seedlings. Interspecific comparisons indicate higher specific leaf area, leaf area ratio, and LMR are commonly associated with greater RGR (Lambers and Poorter 1992; Walters et al. 1993; Reich et al. 1998). In a recent survey of 29 *Pinus* spp., specific leaf area was the primary determinant of RGR, while net assimilation rate and LMR were less important (Grotkopp et al. 2002). Higher RGR of 8-week-old seedlings was associated with reduced investment in stem tissues under low light, and increased allocation to leaf and root production under moderate light. These results suggest that under low light, seedling growth was primarily limited by photosynthetic capacity and LMR. Under moderate light, availability and uptake of belowground resources were more important to seedling growth. Higher RGR in seedlings with larger RMR may have been related to improved nutrient uptake under the more favourable light level, since seedlings were well watered during the study (Lambers and Poorter 1992).

A negative relationship between RGR and seed mass, as observed in 14-week-old white pine seedlings grown under low light, has been reported for several species (Harper et al. 1970; Zimmerman and Weis 1983; Gross 1984; Paz and Martínez-Ramos 2003). In a study of *Xanthium strumarium* L., a herbaceous annual, the higher RGR of seedlings formed from smaller seeds resulted in little difference in size at maturity (Zimmerman and Weis 1983). Within several *Psychotria* spp., a tropical forest tree genus, higher RGR in seedlings from smaller seeds fully compensated for the early seedling growth advantage accrued from heavier seeds under moderate but not low light (Paz and Martínez-Ramos 2003). Despite their slightly higher RGR, white pine seedlings from smaller seeds had much lower total dry mass than seedlings from heavier seeds, evidence supporting our third hypothesis. The comparative influence of a higher RGR on the ability of white pine seedling from small seeds to become established and persist in the shaded forest understory remains to be examined.

Natural variation in seed mass can be viewed as an ecological and evolutionary adaptation to balance reproductive output for both dispersal and establishment and to maximize successful seedling recruitment in a variable environment (Janzen 1977; Michaels et al. 1988). The results of our greenhouse study suggest that when soil resources are nonlimiting, seed mass has a significant positive effect on initial seedling size but little effect on biomass allocation patterns and RGR. Although increased light availability improved growth, expression of seed mass effects was independent of light. Clearly, any further discussion of the ecological role of seed mass on natural regeneration of white

pine beneath closed and partial overstory canopies is premature. The growth period of our study was somewhat shorter than a normal growing season, and only the effects of two light levels on seed mass relationships were examined. As well, these habitats differ in microenvironmental factors (e.g., litter depth, soil temperature, herbivory) other than light intensity that may influence natural regeneration through their effects on the relationship of seed mass with seed germination and seedling establishment. We are currently conducting a 5-year field trial examining the influence of seedbed, overstory canopy density, and seed mass on the emergence, growth, and survival of white pine seedlings. The results of this study should improve our understanding of the ecological role of seed mass on natural regeneration of white pine.

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